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Does biodiversity make a difference? Relationships between species richness, evolutionary diversity, and aboveground live tree biomass across U.S. forests

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ABSTRACT

Biodiversity conveys numerous functional benefits to forested ecosystems, including community stability and resilience. In the context of managing forests for climate change mitigation/adaptation, maximizing and/or maintaining aboveground biomass will require understanding the interactions between tree biodiversity, site productivity, and the stocking of live trees. Species richness may not be the most appropriate tree biodiversity metric in this context as it weights all species as equally important. Measures that account for evolutionary relationships among species should be more biologically meaningful surrogates of functional diversity within forest communities, given that more phylogenetically distinct species should contribute more to the diversity of traits within a community. Using data from approximately 79,000 permanent and standardized forest inventory plots across the United States, we assessed trends in live aboveground tree biomass (LAGB) in relation to metrics of forest tree biodiversity at national and regional scales, controlling for site productivity and live tree stocking. These metrics included four measures of evolutionary diversity associated with distinct components of functional variation. In certain situations and locations across the U.S., evolutionary diversity metrics supply additional information about forest stands beyond that provided by simple species richness counts. This information can potentially include critical insight into tree functional attributes inherently related to evolutionary diversity. Relationships nationally between LAGB and most biodiversity metrics weakened with increasing site productivity and with increasing live tree stocking: The greater the site productivity and tree stocking, the less likely that higher biodiversity was associated with greater LAGB. This is consistent with the expectation that the coexistence of functionally different species increases forest productivity in less productive and more stressful environments, while dominant and highly productive species are able to competitively dominate in more productive habitats. Phylogenetic species clustering (PSC) was increasingly correlated with LAGB as live tree stocking increased on low-productivity sites, suggesting that the co-occurrence of tree species more widely distributed across the phylogenetic tree of life, and therefore likely possessing a wider variety of functional attributes, resulted in greater biomass accumulation on poorer sites. PSC and species richness appear to be the best biodiversity predictors for LAGB on the low-productivity sites likely to be most important for carbon/biomass management. These biodiversity metrics will be important for maximizing biomass/carbon for future carbon sequestration or bioenergy needs and should serve as indicators of forest function in forest resource assessments.

1. Introduction

The fundamental importance of biodiversity to forest management and forest health monitoring at a national scale is recognized by its incorporation into indicators of forest sustainability, including the Criteria and Indicators for the Conservation of Sustainable Management of Temperate and Boreal Forests (Montréal Process Working Group, 2009). Experimental and observational studies have revealed numerous functional benefits of biodiversity to natural ecosystems (Loreau et al., 2001; Hooper et al., 2005; Balvanera et al., 2006). These include attributes of community stability, such as the ability to reduce the susceptibility of the ecosystem to invasion after disturbance (Chapin et al., 1997) and the ability to enhance ecosystem reliability, the probability that the ecosystem will provide a consistent level of performance for a given function over time (Naeem and Li, 1997). A link also exists in many cases

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between ecosystem primary productivity, defined as the rate of plant biomass production (Tilman, 2001), and biodiversity (Naeem et al., 1994; Chapin et al., 2000; Tilman et al., 2001; Cardinale et al., 2007). Much research (e.g., Loreau and Hector, 2001; Gross et al., 2007; Warren et al., 2009) indicates that this relationship can result from "complementarity" between different species that are able to exploit different resources as a result of possessing different traits, ensuring that the efficiency of resource exploitation increases with the addition of new species to a community. One mechanism of complementarity (Loreau and Hector, 2001) is niche differentiation, which is the separation of species by habitat that can result in a more efficient use of resources when a broader range of species traits is present in a more diverse community (Tilman, 1999, 2001). Another complementarity mechanism is facilitation, which occurs when a species modifies the environment in a way that benefits a co-occurring species and which should be more prevalent when greater number of species coexist (Vandermeer, 1989; Fridley, 2001). Biodiversity may also affect ecosystem productivity through the sampling effect, which is the increased statistical probability that, with greater species diversity, species are present that will have a dominant effect on a given community or ecosystem process such as productivity (Huston, 1997; Tilman et al., 1997). Conversely, the coexistence of a greater number of species provides insurance against the loss or poor performance of some species (Folke et al., 1996).

Considering biodiversity in policy and management decision-making is essential, especially when making decisions affecting large temporal and spatial scales (Hooper et al., 2005). One prominent example is the management of forests in the context of climate change, for the fostering of stand resilience to global change through the maintenance of diverse mixtures of tree species and stand structures in managed forest settings (Evans and Perschel, 2009; Puettmann et al., 2009), and for the sequestration of additional atmospheric carbon (Malmsheimer et al., 2008). Recently, forest management strategies for maximizing forest volume or biomass have been applied to the maximization of C sequestration (e.g., even-aged, single-species plantations (Jacobs et al., 2009)). Forest management objectives have long centered on the efficient production of roundwood for sawtimber or pulp markets with periodic harvests on productive timberland (Kimmins, 1992). The increased application of forest management for the purpose of maximizing aboveground C storage or biomass will likely encounter novel combinations of tree species compositions, stand densities, and site qualities. At the same time, factors other than biodiversity are also important in defining ecosystem function (Chapin et al., 1997). Most importantly, the functional characteristics of species present in the ecosystem, and the distribution and abundance of those organisms over space and time, act in concert with climate, resource availability and disturbance regimes to influence ecosystem properties (Hooper et al., 2005). The relationship between biodiversity and productivity, therefore, may vary dynamically over both time and space as a result of spatial heterogeneity and disturbance regimes (Cardinale et al., 2000). Specifically, complementarity mechanisms, such as niche differentiation or facilitation, may allow functionally different species to increase overall productivity in less productive and more stressful environments, while in more productive habitats, dominant and highly productive species are able to competitively exclude others (Warren et al., 2009; Paquette and Messier, 2011).

Better understanding the relationship between tree biodiversity and biomass stocking attributes would greatly aid efforts to estimate the effects that various management activities would have on maximizing aboveground C storage or biomass available to bioenergy industries (Woodall et al., 2011a). In the same manner that past silvicultural research of mixed species systems has informed approaches to management for maximizing merchantable volume yield (e.g., Assmann, 1970; Kelty, 2006), it will be important to determine the effect of tree species composition on biomass production and C storage in response to bioenergy and climate change concerns. This is particularly true across regional scales, where biodiversity is expected to be a less important predictor of ecosystem processes than at smaller spatial scales because biodiversity at large scales is a dynamic variable that adjusts to differences in environmental conditions (Loreau et al., 2001), and where abiotic factors therefore may be the main drivers of variation in ecosystem function across environmental gradients (Loreau, 1998). Although analyses of large numbers of forest plots across Sweden (Gamfeldt et al., 2013), Quebec (Paquette and Messier, 2011), and the Midwest of the United States (Caspersen and Pacala, 2001) found relationships between tree diversity and biomass, such large-scale studies are rare, and none have been conducted for the entire contiguous United States.

Determining indicators of biodiversity that correlate with trends in live aboveground forest biomass (LAGB), in the context of site quality and stand density, would assist in the management forest carbon/biomass across broad scales. Biodiversity is not an easy concept to measure, however (Helmus et al., 2007), and it is not clear whether simple species richness counts are the best tree biodiversity metric when attempting to explain variation in forest productivity (Paquette and Messier, 2011). Species richness is a metric that weights all species equally, and therefore may have more limited value than measures that account for evolutionary relationships among species (Vane-Wright et al., 1991). Taxonomically distinct species are expected to contribute more to the diversity of features, including functional traits, present within a community (Faith, 1992), so measurements of evolutionary history within a set of co-occurring species are assumed to represent the diversity of traits present within that community (Faith, 2002). Greater phylogenetic diversity within communities has been linked to nutrient cycling, resistance to invasion, soil carbon accumulation and other ecosystem processes, goods and services, supporting the argument that phylogenetic diversity is more useful than species richness as a conservation criterion for management decisions (Cavender-Bares et al., 2009). Plant phylogenetic diversity also has been found to explain more variation in community productivity in grasslands than other measures of biodiversity (Cadotte et al., 2008, 2009), while phylogenetic diversity and species richness performed similarly well in explaining forest productivity (Paquette and Messier, 2011). Pillon et al. (2006), meanwhile, demonstrated that phylogenetic diversity is a more appropriate measure of biodiversity than species richness because species richness is more sensitive to taxonomic inflation associated with sampling effort. Comparisons of species richness and phylogenetic diversity across thousands of standardized forest inventory and analysis plots in the United States found that the biodiversity metrics can be strongly correlated across national scales, but that important differences exist regionally and locally (Potter, 2012; Potter and Woodall, 2012).

In order to clarify how and under what circumstances tree biodiversity can serve as a useful indicator of potential forest biomass across broad geographic scales, we used data from approximately 79,000 permanent and standardized forest inventory plots across the contiguous United States to examine the relationship between plot-level measures of biodiversity and levels of LAGB, accounting for site productivity and live tree stocking. Specifically, we tested three hypotheses: (1) Plot-level measures of tree evolutionary diversity are not strongly correlated with species richness across broad scales in the United States; (2) measures of evolutionary diversity are better correlated with levels of forest biomass than species richness, within a matrix of site productivity and live tree stocking; and (3) the relationship between biodiversity and LAGB is stronger when site productivity is lower.

2. Materials and methods

2.1. Data

The Forest Inventory and Analysis (FIA) program of the United States Department of Agriculture (USDA) Forest Service is the primary source for information about the extent, condition, status and trends of forest resources across all ownerships in the United States (Smith, 2002). FIA applies a nationally consistent sampling protocol using a quasi-systematic design to conduct a multiphase inventory of all ownerships; the national sample intensity is approximately one plot per 2428 ha of land (Bechtold and Patterson, 2005). Land area is stratified using aerial photography or classified satellite imagery to increase the precision of estimates using stratified estimation. Remotely sensed data may also be used to determine if plot locations have forest land cover; forest land is defined as areas at least 10% stocked with tree species, at least 0.4 ha in size, and at least 36.6 m wide (Bechtold and Patterson, 2005). Permanent fixed-area FIA inventory plots (approximately 0.067 ha in size) are established in forested conditions when field crews visit plot locations that have accessible forest land. Field crews collect data on more than 300 variables, including forest type, tree species, tree size, tree condition, and site attributes (e.g., slope, aspect, disturbance, land use, land ownership) (Smith, 2002; Woudenberg et al., 2010). The plots consist of four, 7.2-m fixed-radius subplots spaced 36.6 m apart in a triangular arrangement with one subplot in the center (Woudenberg et al., 2010). All trees with a diameter at breast height (dbh) of at least 12.7 cm are inventoried on forested subplots. Trees are defined as woody plants usually having one or more erect perennial stems, a stem diameter at maturity of at least 7.62 cm, a more or less definitely formed crown of foliage, and a height of at least 4.75 m at maturity. Within each subplot, a 2.07 m microplot offset 3.66 m from sub-plot center is established where all live trees with a dbh between 2.5 and 12.7 cm are inventoried. The FIA system is designed so that field crews revisit plots in the eastern United States every five years, with 20% of all plots remeasured every year on a 5-year rotating basis. In the western United States, 10% of plots are remeasured every year on a 10-year rotating basis. Initial annual inventory plots were established in each state between 1999 and 2005.

All inventory data are managed in an FIA database (FIADB, Woudenberg et al., 2010) and are publicly available. Data for this study were taken entirely from the FIADB from plots using the most recent annual inventory in the 48 contiguous states, as of March 2012, for a total of 116,732 unique plot observations. The number of plots used in the study was reduced to 79,324 (Fig. 1) after removing plots that were less than 75% forested or that encompassed more than one site productivity class (i.e., potentially heterogeneous physiography). To account for the effects of site productivity (i.e., site quality) constraints on live aboveground biomass (LAGB), we divided plots into site productivity classes based on FIA site productivity classifications, which identify the potential growth in wood biomass by area per year based on the culmination of mean annual increment of fully stocked natural stands (Woudenberg et al., 2010). The FIA site productivity measures are largely based on the coring of “site index” trees on each inventory plot with subsequent use of regionally specific site index curves to derive a site production potential. We use three site productivity classes: (1) high-productivity, on which the potential for wood growth is greater than 8.4 cubic meters per ha per year (7642 plots); (2) medium-productivity, on which wood growth potential is between 3.5 and 8.4 cubic meters per ha per year (37,390 plots); and (3) low-productivity, on which wood growth potential is less than 3.5 cubic meters per ha per year (34,292 plots).

2.2. Analysis

The focus of this study was to evaluate how different biodiversity metrics predict LAGB on FIA plots across the contiguous 48 United States. LAGB was determined for each of the 79,324 plots following a series of procedures. First, individual tree gross volume was calculated based on regional volume equations (Woodall et al., 2011b). Second, each tree’s sound volume was calculated based on regional volume equations along with merchantable stem deductions (through tree class code in FIADB) due to rough, rotten, and missing portions of the tree. Third, the sound volume was converted to bole oven-dry biomass using species-specific wood density values (Miles and Smith, 2009; Woudenberg et al., 2010). Fourth, total tree oven-dry biomass was calculated using the Component Ratio Method (CRM, Woodall et al., 2011b). Briefly, the CRM facilitates calculation of tree component biomass (e.g., tops and limbs) as a proportion of the bole (i.e., central stem) biomass based on component proportions from Jenkins et al. (2003).

We calculated species richness (SR) and four evolutionary diversity statistics as plot-level metrics of biodiversity. All plot-level evolutionary diversity metrics were calculated using the R 2.14.1 program Picante (Kembel et al., 2010) and a hypothesized phylogenetic supertree of 311 North American forest tree species included in the FIA database (Appendix A). The first of the evolutionary metrics, phylogenetic diversity (PD) (Faith, 1992), is the minimum spanning distance (sum of all branch lengths) of a phylogenetic tree representing all the species from a given plot, measured in millions of years of evolutionary time. It is conceptually simple, widely used, and among the first such metrics to be developed. The other three evolutionary diversity metrics were described by Helmus et al. (2007) as part of an integrated and relatively easy-to-understand package of phylogenetic measures of species variability, richness and evenness with well-defined statistical properties. These were:

- Phylogenetic species variability (PSV), which is statistically independent of species richness and quantifies how phylogenetic relatedness decreases the variance of a hypothetical trait shared by all the species in a community. As a measure of the deviation from a star phylogeny, it is an index that approaches 1 as species are less closely related, and 0 as the species are more closely related.
- Phylogenetic species evenness (PSE), which is similar to PSV (again, a measure of the deviation from a star phylogeny) but modified to incorporate relative species abundances (here, stems per FIA plot). It approaches 1 when species abundances are equal and species are highly unrelated, and approaches 0 with highly different abundances of species that are closely related. It is therefore a measure of both species and phylogenetic evenness.
- Phylogenetic species clustering (PSC), which quantifies the branch-tip clustering of species across the phylogenetic tree. As it approaches 1, species are less related to one another at the tips of the phylogenetic tree.

An additional metric described by Helmus et al. (2007), phylogenetic species richness (PSR), was not included in our analysis because of its similarity to and high degree of correlation with PD ($r > 0.97$ for plots in each of the three site productivity classes).

To assess the relationship between biodiversity metrics and LAGB, it was necessary to control for stand stocking because a forest stand’s level of biomass is dependent on its stocking of live trees (i.e., proximity to self-thinning line) as well as its site productivity (Oliver and Larson, 1996). We defined live tree stocking as the number of trees per unit area currently in a stand relative to the maximum potential possible (relative density [RD], Appendix

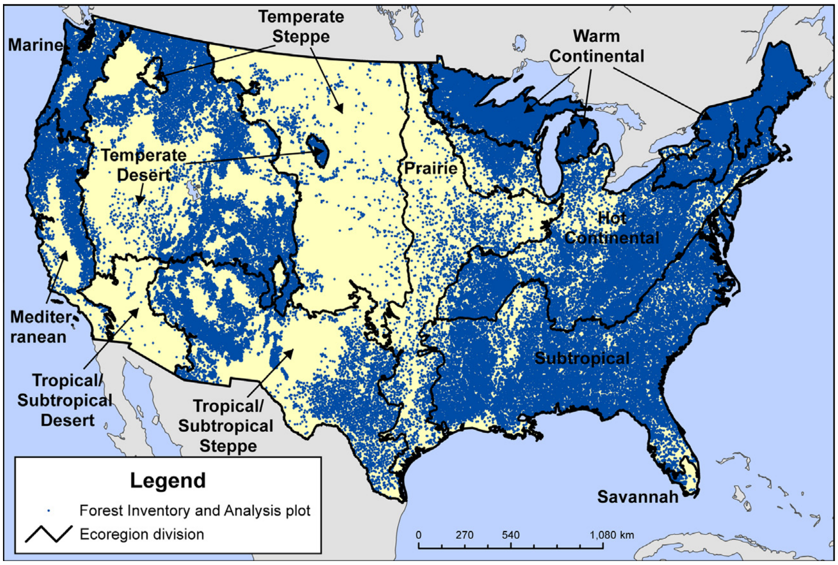

Fig. 1. The 79,324 Forest Inventory and Analysis (FIA) plots included in the study from across the contiguous United States, within each of 11 ecoregion divisions. Each plot is about 0.067 ha in area; locations are approximate.

B). We acknowledge that stands can have the same RD at different stages of stand development; however, RD should broadly account for the effect of stand stocking on potential levels of LAGB across large-scales.

We controlled for RD when determining how closely the five biodiversity measures were associated with each other, using PROC CORR in SAS 9.2 (SAS Institute Inc., 2008) to test for partial Pearson correlations between each pair of biodiversity metrics within each of the three site productivity classes. We did this both nationally and within ecoregion divisions, after using ArcMap 10.0 (ESRI, 2010) to assign each plot to the appropriate ecoregion based on the most recent geographic information system (GIS) mapping of ecoregions by the USDA Forest Service (Cleland et al., 2007) (Fig. 1). Divisions are determined based on large ecological climate zones, and are among the broader ecoregions in a hierarchical system (Bailey, 1995). Ecoregion divisions were excluded from a given analysis when they contained fewer than 50 FIA plots.

To determine the extent to which relationships between LAGB and biodiversity were linear, we used PROC REG in SAS 9.2 (SAS Institute Inc., 2008) to compare regression models in which the biodiversity metrics were untransformed (linear), in which they were squared (quadratic), and in which both the untransformed and quadratic terms were included. The models were ranked using Akaike's Information Criterion (AIC) (Akaike, 1974). We conducted this analysis within site productivity classes, after separating plots into stand stocking classes roughly related to classes of stand occupancy (Long and Daniel, 1990) (high: RD between 0.66 and 1.0; medium, RD greater than 0.33 and less than 0.66; low, RD between 0 and 0.33). Combinations of RD and site quality classes therefore resulted in nine unique model comparisons, each comparing three regression models. Woodall et al. (2011a) found RD to be as a useful metric of interspecific stand stocking when examining maximization of forest C stocks in the eastern U.S.; however, they did not incorporate measures of site quality or explicit measures of biodiversity in their study. We also used PROC CORR in SAS to calculate correlations between biodiversity metrics and LAGB to assess the direction (positive or negative) and strength of these relationships.

Finally, we generated best subsets multiple linear regression models using PROC REG in SAS 9.2 (SAS Institute Inc., 2008) to determine which combinations of biodiversity metrics, along with RD, best predict plot-level LAGB within site productivity classes. We generated and assessed collinearity diagnostics in PROC REG for each site productivity class, removing the quadratic terms for each biodiversity metric because of high apparent collinearity between the linear and quadratic terms. The multiple linear regression models within each site productivity class were then ranked using Akaike's Information Criterion (AIC) (Akaike, 1974), both nationally and within ecoregion divisions.

3. Results

3.1. Relationships among biodiversity metrics

Mean plot live aboveground biomass (LAGB) and biodiversity metrics were broadly examined by classes of site productivity and relative density (RD) across the forests of the contiguous United States. LAGB increased by classes of site productivity and RD (Table 1). Mean biodiversity metrics across plots were generally higher with greater RD within productivity classes. High- and medium-productivity plots had higher mean values for the biodiversity metrics, although species richness (SR), phylogenetic diversity (PD), and phylogenetic species clustering (PSC) were highest on medium-productivity plots.

The degree of correlation between biodiversity metrics varied by site productivity across all U.S. forests when controlling for RD (Table 2). The correlation between SR and most of the four evolutionary diversity metrics was strongest on the highest productivity sites, and weakest on the medium-productivity sites. The exception was the correlation between SR and phylogenetic species variation (PSV), which was positive on low-productivity plots, non-significant on medium-productivity plots, and negative on high-productivity plots. SR and PD were highly correlated ($r > 0.85$) across site productivity classes. The strength of the relationship between PD and both PSV and phylogenetic species evenness (PSE), as well as between PSV and PSE, decreased with increasing site productivity. The relationship between PSC and both PD and PSE was strongest on high-productivity plots and weakest on medium-productivity plots. The relationship between PSC and PSV was positive on low-productivity plots, and weakly negative on medium- and high-productivity sites. PD had the highest mean correlation with the other biodiversity metrics across site productivity classes, while PSV had the lowest.

Table 1
Mean and standard deviation for live tree aboveground biomass (LAGB) and each of five biodiversity metrics across Forest Inventory and Analysis plots.

Site productivity	Relative density	Plots	LAGB		SR		PD		PSV		PSE		PSC	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Low	Low	14,918	10.14	11.05	2.40	1.75	549.5	249.9	0.390	0.353	0.290	0.286	0.291	0.299
	Medium	14,562	36.69	22.46	4.67	2.90	806.6	316.4	0.514	0.256	0.376	0.227	0.514	0.266
	High	4812	56.22	35.21	4.59	2.91	828.1	333.5	0.547	0.260	0.388	0.236	0.488	0.262
Medium	Low	10,520	18.79	16.44	3.96	2.49	727.5	304.2	0.460	0.284	0.360	0.242	0.485	0.288
	Medium	20,242	50.06	23.17	6.65	3.08	997.4	323.7	0.503	0.192	0.402	0.182	0.639	0.188
	High	6628	85.33	45.86	6.97	3.21	1070.0	334.7	0.542	0.180	0.429	0.185	0.633	0.170
High	Low	1757	23.49	29.31	3.60	2.47	719.7	307.4	0.499	0.326	0.369	0.266	0.392	0.297
	Medium	3847	60.18	33.18	5.93	3.28	980.6	333.1	0.570	0.227	0.428	0.203	0.551	0.239
	High	2038	128.76	89.70	5.51	3.18	985.8	339.1	0.615	0.211	0.438	0.212	0.523	0.215

SR, species richness; PD, phylogenetic diversity; PSV, phylogenetic species variability; PSE, phylogenetic species evenness; PSC, phylogenetic species clustering.

Table 2
Partial correlations between biodiversity metrics across Forest Inventory and Analysis plots within site productivity classes, controlling for stand relative density. Correlations significant at $p < 0.05$ are in bold.

	Site productivity														
	Low					Medium					High				
	SR	PD	PSV	PSE	PSC	SR	PD	PSV	PSE	PSC	SR	PD	PSV	PSE	PSC
SR	.	***0.870***	***0.169***	***0.306***	***0.684***	.	***0.860***	−0.009	***0.286***	***0.589***	.	***0.888***	***−0.072***	***0.324***	***0.690***
PD		.	***0.513***	***0.573***	***0.525***		.	***0.371***	***0.562***	***0.378***		.	***0.261***	***0.543***	***0.548***
PSV			.	***0.819***	***0.139***			.	***0.703***	***−0.093***			.	***0.581***	***−0.095***
PSE				.	***0.503***				.	***0.364***				.	***0.547***
PSC					.					.					.
Mean	0.507	0.620	0.410	0.550	0.463	0.431	0.543	0.243	0.479	0.309	0.458	0.560	0.169	0.499	0.422

SR, species richness; PD, phylogenetic diversity; PSV, phylogenetic species variability; PSE, phylogenetic species evenness; PSC, phylogenetic species clustering.

Within ecoregion divisions, the partial correlations between SR and PD, controlling for stand relative density, were consistently strong across the contiguous United States, but strongest in the Interior West ($r > 0.90$) (Fig. 2A, Appendix Table A.1). More geographical variation was apparent in the relationships between SR and the other evolutionary diversity metrics. With PSV, for example, the relationships generally were weaker in the East and stronger in the West; the partial correlations varied from $r = -0.006$ in the Subtropical division in the Southeast to $r = 0.892$ in the Tropical/Subtropical Desert of the Southwest (Fig. 2B). A similar pattern existed for PSE (Fig. 2C): the eastern Hot Continental division had the weakest correlation with SR ($r = 0.273$) while the Tropical/Subtropical Desert division had the highest ($r = 0.848$). For PSC, however, the relationship with SR was generally stronger in the more southerly ecoregions than those in the North (Fig. 2D). The partial correlation for the Hot Continental ecoregion was weak ($r = 0.382$), while that for the Savannah of the Southeast was relatively strong ($r = 0.779$).

3.2. Relationships between biomass and biodiversity

The results of our model comparison analysis suggest that the relationships between live aboveground biomass and the biodiversity metrics are generally linear or slightly curvilinear within most site productivity/relative density combinations (Table 3, Figs. 3 and 4). Specifically, univariate regression models in which the biodiversity metrics were untransformed (linear models) had higher adjusted R^2 values and lower AIC values than models in which the biodiversity models were squared (quadratic models) (Table 3). The only exceptions were for phylogenetic species variability (PSV) and phylogenetic species evenness (PSE) on low- and medium-productivity sites with medium relative density, and for phylogenetic species clustering (PSC) on high-productivity sites with high relative density. The best regression models were typically those that included both the untransformed and quadratic terms, although models containing only the untransformed phylogenetic diversity (PD) metric were the best models in some cases. In general, the results indicate less variation in biodiversity on plots with higher productivity and with higher relative density (Figs. 3 and 4).

Correlations between LAGB and most biodiversity metrics across all plots weakened with increasing site productivity and with increasing stand relative density (RD) (Table 4), becoming significantly and considerably negative on medium-productivity plots with high RD, and on high-productivity plots with medium or high density. In other words, the higher the productivity of the site and the greater the relative density of the stand, the less likely that higher biodiversity was associated with greater LAGB. There were important exceptions to this trend. For example, while PSC decreased with greater stand RD on medium- and high-quality sites, it actually increased with greater stand RD on low-quality sites. PSV and PSE, meanwhile, generally exhibited the least positive correlations with LAGB on plots on medium site quality and medium stand density. Among the biodiversity metrics, SR had the strongest relationship with LAGB on low-density stands on sites of low or medium quality. It was also the most strongly associated with LAGB, negatively, on high-productivity, high-density sites. PSC was the biodiversity metric most strongly correlated with LAGB on low-productivity plots with either medium or high RD, as well as on medium-productivity sites with medium RD. PD was the metric most strongly correlated with LAGB on high-productivity, low-density plots, and, negatively, on medium-productivity, high-density plots. PSE, finally, was the only biodiversity metric significantly positively correlated with LAGB on high-productivity, medium-density plots.

Because SR and PSC were the biodiversity metrics most strongly associated with LAGB nationally, we mapped partial correlations between these metrics and LAGB in each of the ecoregion divisions, controlling for stand RD. These maps indicate important regional

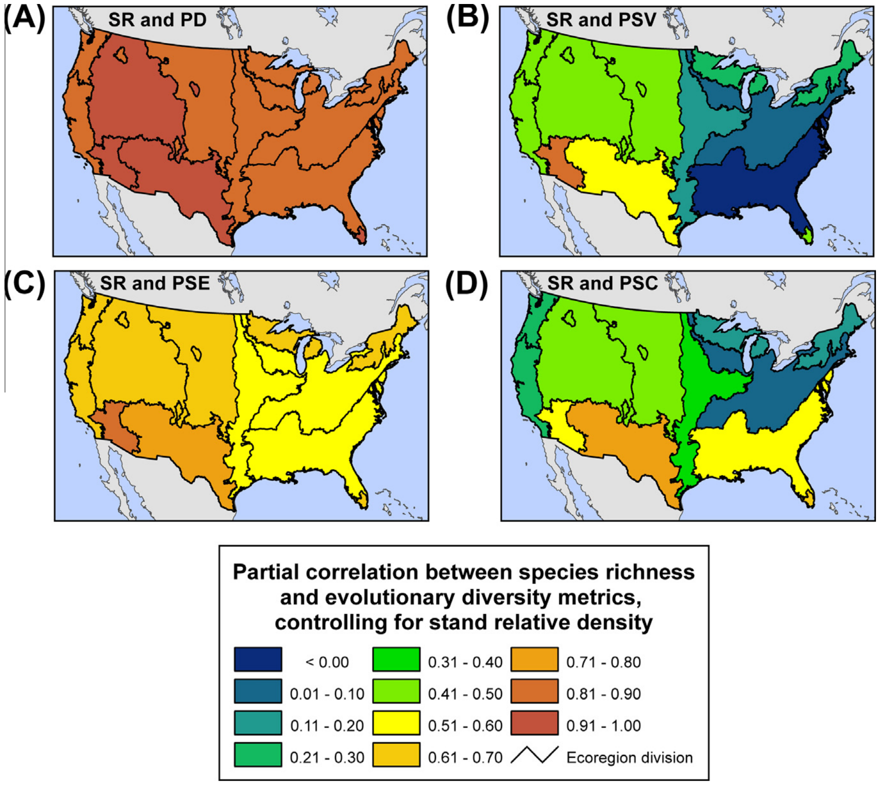

Fig. 2. Partial correlations across Forest Inventory and Analysis (FIA) plots within ecoregion divisions of species richness (SR) with (A) phylogenetic diversity (PD), (B) phylogenetic species variability (PSV), (C) phylogenetic species evenness (PSE), and (D) phylogenetic species clustering (PSC). The partial correlations control for stand relative density within plots. For ecoregion division names, see Fig. 1.

differences in the association of SR and PSC with LAGB (partial correlations for all ecoregion divisions are presented in Appendix Table A.2). For sites with low productivity, SR had higher partial correlations in four low latitude ecoregions: Mediterranean, Tropical/Subtropical Desert, Tropical/Subtropical Steppe, and Subtropical, while PSC had higher partial correlations in two more northerly ecoregions: Temperate Desert and Warm Continental (Fig. 5A and B). In other ecoregions, the partial correlations were approximately the same, or not significant for both biodiversity metrics. For medium-productivity sites, SR had a stronger partial correlation than PSC in only the Subtropical ecoregion ($r = 0.214$ for SR, $r = 0.199$ for PSC) (Figs. 5C and 3D). For the Warm Continental ecoregion, PSC was considerably more strongly associated with LAGB ($r = 0.142$ for PSC, $r = 0.038$ for SR). It was also significantly positively correlated with LAGB in the Temperate Desert ecoregion and significantly negatively correlated for the Marine and Temperate Steppe ecoregions, but the correlations were weak. Finally, for high-productivity sites, SR was negatively correlated with LAGB for the Temperate Desert (Fig. 5E), while PSC was positively correlated with LAGB for the Hot Continental and Warm Continental regions. Both metrics were positively associated with LAGB for the Subtropical region (Fig. 5F).

3.3. Linear regression models

We generated multiple linear regression models within site productivity classes nationally and within ecoregions to compare the explanatory power of the best models, containing relative density and all or most of the biodiversity metrics, with those containing fewer independent variables. Overall, the lower the site quality, the more variation in live aboveground biomass (LAGB) was explained by the biodiversity metrics and relative density (Table 5). The adjusted R^2 values for the full models, for example, declined with site productivity (low productivity, adjusted $R^2 = 0.555$; medium productivity, adjusted $R^2 = 0.487$; high productivity, adjusted $R^2 = 0.428$). On low-productivity sites, adding more independent variables improved the multiple linear regression models. On medium- and high-productivity sites, however, little extra explanatory power resulted from adding more biodiversity metrics, suggesting that tracking only relative density and two biodiversity metrics would allow for the explanation of nearly as much variation in LAGB as when using all the biodiversity metrics in the best models. Within most ecoregion divisions, the explanatory power of the models also decreased as site productivity increased (Table 6). The exceptions were the Savannah, Temperate Desert and Temperate Steppe ecoregions, for which the models for higher-productivity sites explained more variation in LAGB than those for low-productivity sites. For two ecoregions, Mediterranean and Prairie, no biodiversity metrics – only relative density – were included in the best models for high-productivity sites. The models, across site productivity classes, generally accounted for at least half of the variation in LAGB.

4. Discussion

The results of this study suggest that evolutionary diversity metrics may refine our understanding of forest dynamics in the context of woody biomass production in a way not possible when considering only species richness (SR). The partial correlations between SR and some evolutionary diversity metrics (phylogenetic diversity [PD] and phylogenetic species clustering [PSC]) exceeded 0.5, but were considerably lower for others (phylogenetic species variability [PSV] and phylogenetic species evenness [PSE]). Species richness was most highly correlated with PD, but even this corre-

Table 3
Adjusted R^2 values from regression models between live aboveground tree biomass (LAGB) and biodiversity metrics within site productivity/stand relative density combinations across Forest Inventory and Analysis plots. Three models are compared for each combination, with the biodiversity metric untransformed (linear), with a squared quadratic term for the biodiversity metric, and with both together. Models with lowest Akaike's Information Criterion (AIC) values are in bold.

Relative density (RD)		Site productivity														
		Low					Medium					High				
		SR	PD	PSV	PSE	PSC	SR	PD	PSV	PSE	PSC	SR	PD	PSV	PSE	PSC
Low	Linear	0.249	**0.164**	0.030	0.023	0.177	0.110	0.080	0.009	0.008	0.071	0.045	0.055	0.023	0.009	0.042
	Quadratic	0.207	0.154	0.005	0.002	0.165	0.093	0.071	0.000	0.000	0.060	0.029	0.046	0.007	0.001	0.030
	Linear plus quadratic	**0.251**	0.164	**0.138**	**0.112**	**0.177**	**0.111**	**0.081**	**0.077**	**0.070**	**0.072**	**0.054**	**0.057**	**0.059**	**0.035**	**0.049**
Medium	Linear	0.190	0.099	0.014	0.002	0.225	0.010	0.000	0.013	0.000	0.024	**0.001**	0.001	0.000	0.007	0.000
	Quadratic	0.134	0.080	0.055	0.021	0.225	0.007	0.000	0.025	0.004	0.019	0.001	0.001	0.000	0.005	0.000
	Linear plus quadratic	**0.223**	**0.111**	**0.171**	**0.112**	**0.229**	**0.012**	**0.005**	**0.042**	**0.027**	**0.024**	0.001	**0.001**	**0.001**	**0.007**	**0.005**
High	Linear	0.146	0.074	0.052	0.000	0.241	0.018	0.021	0.002	0.000	0.004	0.088	**0.058**	0.003	0.000	0.040
	Quadratic	0.092	0.055	0.011	0.013	0.227	0.014	0.020	0.002	0.001	0.006	0.072	0.055	0.007	0.002	0.063
	Linear plus quadratic	**0.192**	**0.093**	**0.189**	**0.106**	**0.241**	**0.020**	0.021	**0.002**	**0.003**	**0.009**	**0.092**	0.057	**0.013**	**0.006**	**0.079**

SR, species richness; PD, phylogenetic diversity; PSV, phylogenetic species variability; PSE, phylogenetic species evenness; PSC, phylogenetic species clustering.

lation was variable across regions of the United States. Specifically, the evolutionary diversity metrics were less correlated with species richness in eastern parts of the country, where the widespread existence of mixed hardwood-conifer forests may result in greater evolutionary diversity than expected given species richness. In contrast, other regions of the U.S. exhibited higher correlations between species richness and evolutionary diversity metrics; this includes the relative species-poor and conifer-dominated ecoregions of the Southwest. It appears that basic knowledge of tree species mixtures across large-scales can inform the appropriate use of evolutionary diversity metrics. These results are consistent with past analyses, which found that while PD and species richness have similar distributions when quantifying forest biodiversity, important differences exist between the two, particularly at small scales and with clear geographic trends among ecoregions defined by geology, climate and soils (Potter, 2012; Potter and Woodall, 2012). The application of evolutionary diversity metrics rather than or in addition to species richness in evaluations of forest biodiversity and forest dynamics seems appropriate, at least in some circumstances, given the decoupling of the two types of indices at small to medium scales (e.g., ecoregion or sub-ecoregion), and their imperfect relationship at large scales.

Perhaps more importantly, evolutionary history metrics are expected to better represent variation in the functional traits present in a community, at least in some cases (Faith, 2002; Forest et al., 2007; Cadotte et al., 2008, 2009). While phylogenies do not perfectly reflect the relationships among species in physiological and ecological attributes that affect their roles within and impacts on communities, and while nonlinear relationships are possible between evolutionary time and ecological differences (including differential rates of evolutionary change over time), phylogenetic relatedness provides an easily applied surrogate for understanding how communities are structured (Helmus et al., 2007). Additionally, the evolutionary diversity metrics we include in this study address the three primary components of functional diversity: functional richness (the amount of niche space filled by species in the community), functional evenness (the evenness of abundance distribution in filled niche space) and functional divergence (the degree to which the distribution in niche space maximizes divergence in functional characteristics within the community) (Mason et al., 2005). Phylogenetic diversity (PD) is an indicator of functional richness, phylogenetic species evenness (PSE) is an indicator of functional evenness, and phylogenetic species variability (PSV) and phylogenetic species clustering (PSC) are indicators of different aspects of functional divergence. Specifically, PSV is useful for quantifying tree-wide phylogenetic structure, encapsulating broad similarities and differences among species, because it measures pure phylogenetic signal not confounded by species richness and abundance, while PSC is PSV modified to measure phylogenetic clustering of species across the tips of a phylogeny (Helmus et al., 2007). It is not surprising, therefore, that partial correlations among these evolutionary diversity metrics, both nationally and within ecoregions, are often weak and sometimes negative.

The strength of the relationships between live aboveground biomass (LAGB) and all five biodiversity metrics declined with increasing site productivity, suggesting that complementarity mechanisms (e.g., niche partitioning and facilitation) became less important as the quality of the site improved. On low-quality sites, tree communities possessing greater species richness, PD and PSC were able to accumulate greater amounts of biomass than communities with lower biodiversity values, possibly because the species possess additional functional variation that enhances biomass accumulation within high-diversity stands (Caspersen and Pacala, 2001). Meanwhile, higher-quality sites had greater overall live aboveground biomass, species richness, and PD on average, but the amount of biomass variation on higher-quality sites explained

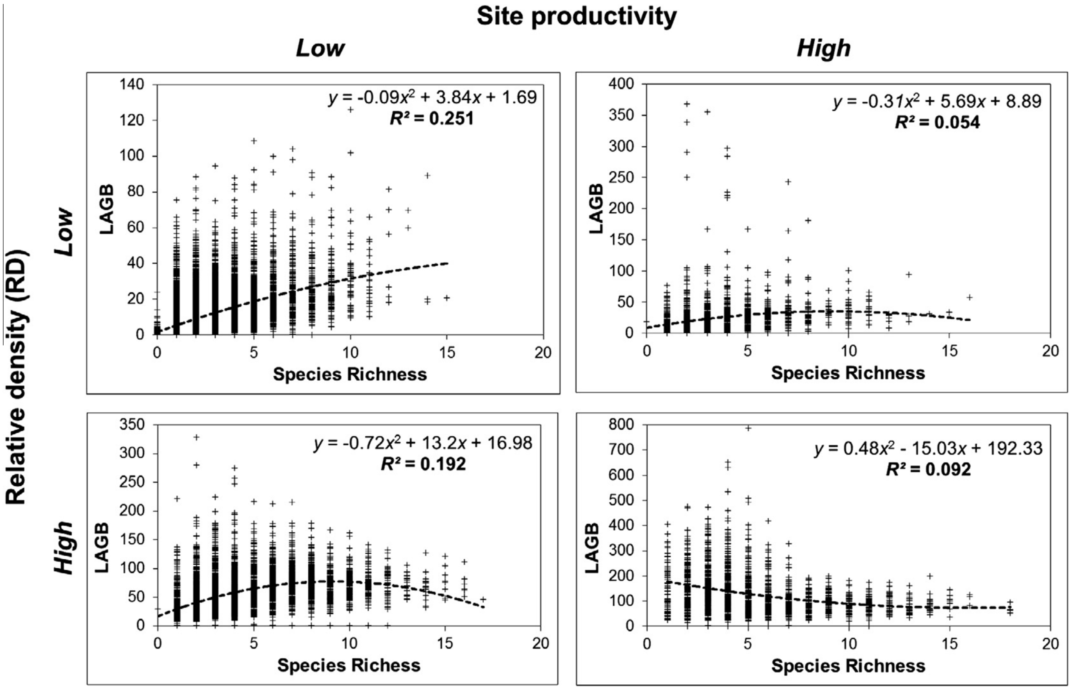

Fig. 3. Scatterplots of species richness (SR) and live aboveground biomass (LAGB) for Forest Inventory and Analysis (FIA) plots with combinations of low and high site productivity and low and high relative density. Note the differences in the scale of the *y*-axes. Best regression models, R^2 values and trendlines are included for each combination.

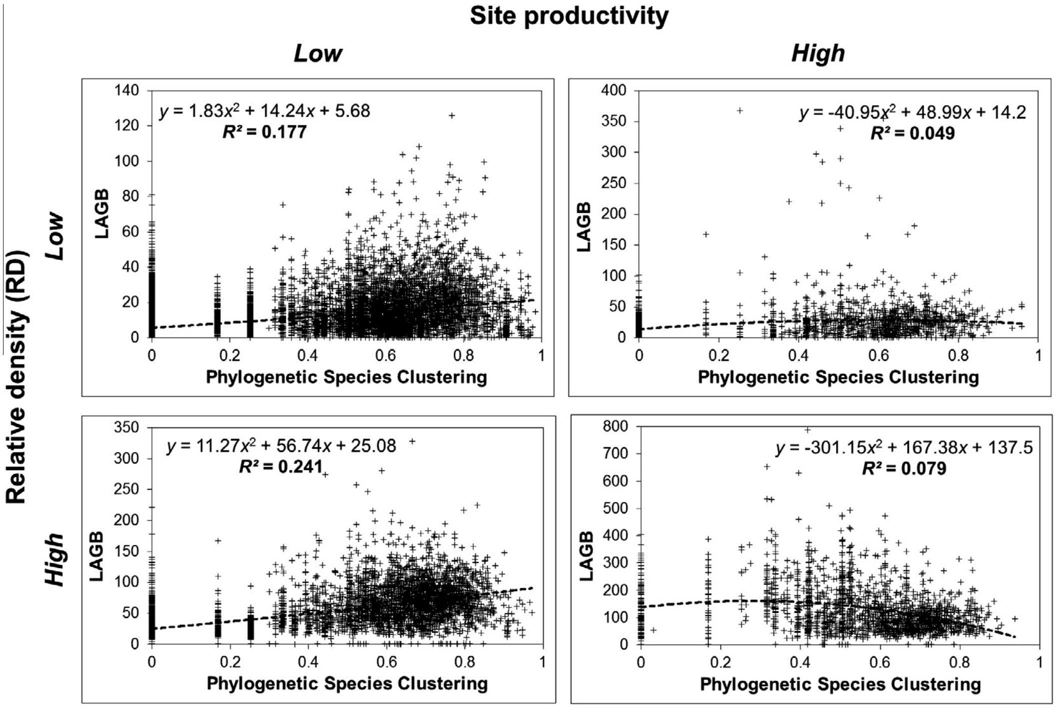

Fig. 4. Scatterplots of phylogenetic species clustering (PSC) and live aboveground biomass (LAGB) for Forest Inventory and Analysis (FIA) plots with combinations of low and high site productivity and low and high relative density. Note the differences in the scale of the *y*-axes. Best regression models, R^2 values and trendlines are included for each combination.

by biodiversity metrics was much less than on low-quality sites, and in many cases the amount of variation in biomass explained by biodiversity was negligible. Additionally, most biodiversity metrics were negatively correlated with live aboveground biomass on plots with medium or high site productivity and high stand stocking, suggesting that a limited number of species well-adapted to the local conditions may better accumulate woody biomass on good sites than mixtures of evolutionarily diverse species. These findings add weight to the expectation that interspecific competitive exclusions, rather than interspecific complementarity, are more dominant with increasing ecosystem productivity (Warren et al., 2009).

Table 4
Correlations between live aboveground tree biomass (LAGB) and biodiversity metrics within site productivity/stand relative density combinations across Forest Inventory and Analysis plots. Correlations significant at $p < 0.05$ are in bold.

Relative density (RD)	Site productivity														
	Low					Medium					High				
	SR	PD	PSV	PSE	PSC	SR	PD	PSV	PSE	PSC	SR	PD	PSV	PSE	PSC
Low	***0.499***	***0.405***	***0.173***	***0.153***	***0.420***	***0.332***	***0.283***	***0.094***	***0.090***	***0.266***	***0.213***	***0.235***	***0.155***	***0.100***	***0.206***
Medium	***0.436***	***0.314***	***−0.117***	***−0.042***	***0.474***	***0.099***	***0.019***	***−0.116***	***−0.018***	***0.154***	−0.031	***−0.033***	−0.008	***0.082***	0.008
High	***0.382***	***0.272***	***−0.103***	−0.018	***0.491***	***−0.136***	***−0.147***	***−0.041***	−0.014	***−0.060***	***−0.297***	***−0.241***	***0.062***	0.030	***−0.201***

SR, species richness; PD, phylogenetic diversity; PSV, phylogenetic species variation; PSE, phylogenetic species evenness; PSC, phylogenetic species clustering.

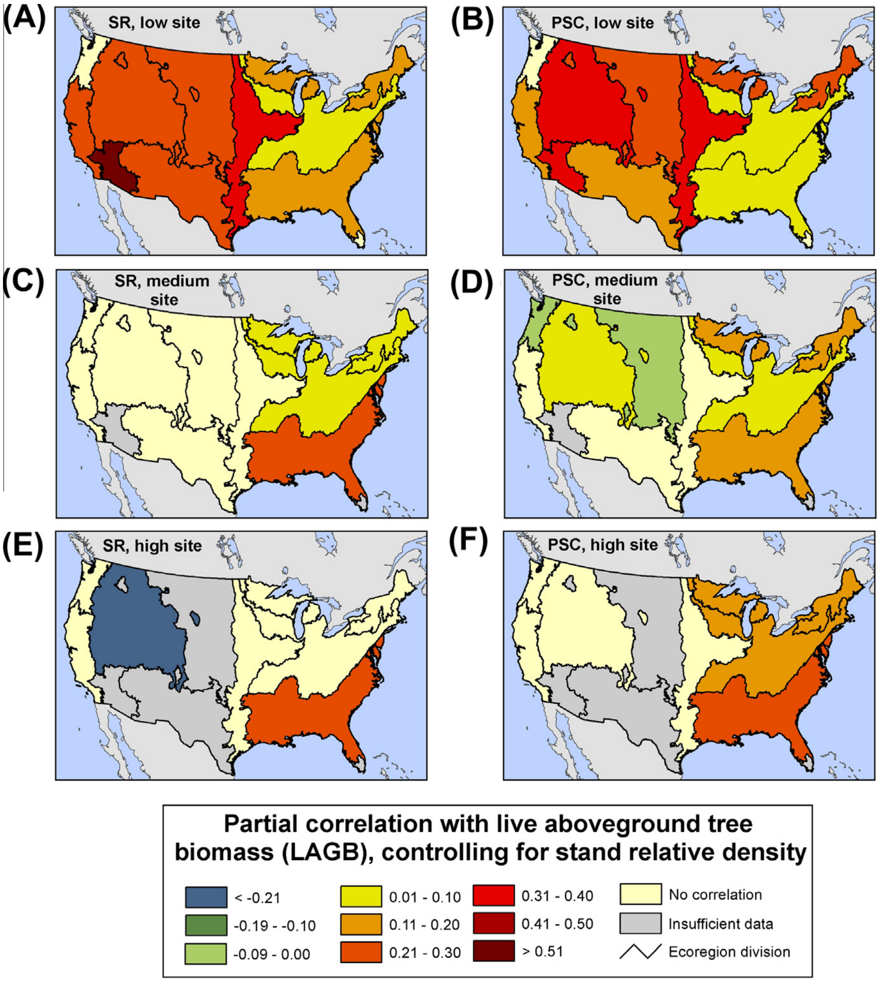

Fig. 5. Partial correlations across Forest Inventory and Analysis (FIA) plots within ecoregion divisions of live aboveground tree biomass (LAGB) with species richness (SR) and phylogenetic species clustering (PSC) on low-productivity sites (A and B), medium-productivity sites (C and D), and high-productivity sites (E and F). The partial correlations control for stand relative density within plots. For ecoregion division names, see Fig. 1.

In the context of stand stocking (relative density [RD]), we found important differences in the amount of biomass variation explained by types of biodiversity metrics, and in the direction of the relationships between live aboveground biomass and those metrics. On low-productivity sites, for example, indicators of functional richness (species richness and phylogenetic diversity) explained more variation in biomass on less-densely stocked than on more-densely stocked sites, while the reverse was true for indicators of functional divergence (phylogenetic species variability and phylogenetic species clustering), which explained more biomass variation on more-densely stocked sites (Table 3). This appears to demonstrate that functional richness may be more important for accumulating woody biomass on poor sites when stand stocking is low, such as when a stand is in early stages of development, while functional divergence is more important for accumulating woody biomass in more densely stocked stands, including those in later stages of development. Interestingly, the two metrics of functional divergence (PSC and PSV) expressed different relationships with biomass across stand density classes on low-productivity sites. Specifically, the correlation between PSC and live aboveground biomass was positive and increased with stand stocking on poorer sites, suggesting that tree species that were more widely distributed across the tips of the phylogenetic tree (i.e., likely possessing a wider variety in functional attributes)

Table 5

Best sub-sets multiple linear regression predictor models of live aboveground biomass (LAGB), by site productivity classes; ranks for models with three or fewer independent variables are based on Akaike's Information Criterion. All models are significant at $p < 0.0001$.

Site productivity	Intercept	RD	SR	PD	PSC	PSV	PSE	DF	Adj. R^2	AIC
Low										
Best model	−6.16	59.27	2.3		16.62	−4.06	−7.98	34,291	0.555	232347
Best with <= 3 variables	−8.95	57.88	2.1		16.14			34,288	0.542	198991
	−1.61	61.11	5.3	−0.020				34,288	0.539	199271
	−5.05	59.98	3.7				−11.59	34,288	0.538	199325
Medium										
Best model	1.84	112.19	0.9	−0.016	4.93	−8.88	13.39	37,383	0.487	241050
Best with <= 3 variables	3.29	111.37	1.4	−0.016				37,386	0.483	241283
	−2.16	110.78		−0.007	10.16			37,386	0.483	241299
	1.12	110.50				−14.79	8.52	37,386	0.482	241354
High										
Best model	−6.09	179.28	−4.0		4.94	−17.61	32.80	7636	0.428	59,784
Best with <= 3 variables	−2.30	180.01		−0.036			33.92	7638	0.426	59,815
	−10.31	176.71	−3.4				19.77	7638	0.425	59,819
	−6.81	177.38	−3.4		9.37			7638	0.422	59,863

RD, stand relative density; SR, species richness; PD, phylogenetic diversity; PSV, phylogenetic species variability; PSE, phylogenetic species evenness; PSC, phylogenetic species clustering.

Table 6

Best multiple linear regression predictor models of live aboveground biomass (LAGB) within ecoregion divisions, by site productivity classes, based on Akaike's Information Criterion. All models are significant at $p < 0.05$.

Ecoregion division	Site productivity	*N*	Intercept	RD	SR	PD	PSC	PSV	PSE	df	Adj. R^2
Hot Continental	Low	4966	−1.76	101.02	0.2		6.99	−7.54		4961	0.539
	Medium	9779	−0.81	113.40	−0.6	0.006	6.92	−22.05	8.99	9772	0.527
	High	958	−5.42	115.53	−3.1	0.022	36.47	−28.05		952	0.486
Marine	Low	607	−13.56	142.76			8.64	−19.77	26.09	602	0.651
	Medium	1017	−22.68	218.66	−6.8	0.032				1013	0.620
	High	1558	−23.97	258.93				−15.94		1555	0.563
Mediterranean	Low	1476	−8.16	85.27	5.9			−10.89		1472	0.645
	Medium	1334	2.30	155.45					−15.54	1331	0.525
	High	742	−12.55	209.14						740	0.368
Prairie	Low	1103	−2.39	49.38	2.5	−0.008	5.28			1098	0.546
	Medium	989	−0.92	89.46			5.44			986	0.557
	High	56	6.73	86.13						54	0.427
Savannah	Low	70	−11.36	61.65	−5.9	0.041				66	0.733
	Medium	27	0.22	45.55	2.6					24	0.779
	High	0				No plots in this site productivity class					
Subtropical	Low	1938	−2.76	82.48	1.1			−5.30		1934	0.589
	Medium	12,548	−1.31	84.72	2.4	−0.016	5.31	−5.21	9.43	12,541	0.527
	High	3688	6.07	81.88	4.1	−0.030			19.46	3683	0.463
Temperate Desert	Low	8724	1.60	44.94	7.7	−0.024	13.08		−11.67	8718	0.426
	Medium	3213	8.43	119.03	4.7	−0.036			5.76	3208	0.612
	High	246	5.64	198.22		−0.032				243	0.732
Temperate Steppe	Low	907	2.53	42.42	9.4	−0.030	−5.57		−5.21	901	0.525
	Medium	143	3.05	134.76		−0.028			19.92	139	0.592
	High	17				Insufficient plots in this site productivity class					
Tropical/Subtropical Desert	Low	93	1.06	16.51	32.1	−0.102	−29.03		3.19	87	0.838
	Medium	0				No plots in this site productivity class					
	High	0				No plots in this site productivity class					
Tropical/Subtropical Steppe	Low	7378	−4.77	29.00	1.7	0.007	−1.94		−3.10	7372	0.524
	Medium	227	13.43	83.88			7.82		−14.58	273	0.486
	High	17				Insufficient plots in this site productivity class					
Warm Continental	Low	7030	−1.85	81.42	3.9	−0.029	12.68		6.73	7024	0.595
	Medium	8063	5.53	88.11	3.1	−0.028	4.34	−4.37	12.13	8056	0.535
	High	377	3.26	87.25	3.4	−0.035	11.80		21.07	371	0.492

RD, stand relative density; SR, species richness; PD, phylogenetic diversity; PSV, phylogenetic species variability; PSE, phylogenetic species evenness; PSC, phylogenetic species clustering.

were able to accumulate more biomass on poorer sites through the progression of stand development. The correlation between PSV and live aboveground biomass, meanwhile, was positive on low-density sites and negative on medium- and high-density sites with low productivity. This may indicate that greater woody biomass production results from niche partitioning of site resources associated with basal (e.g., conifer vs. hardwood) evolutionary differences on low-density (potentially regenerating) sites but not on higher-density (potentially in advanced stages of stand development) sites. The fact that the negative correlations between PSV and live aboveground biomass were considerably weaker than the positive correlations between PSC and live aboveground biomass under the same conditions suggests branch-tip clustering exerts more of an influence on woody biomass accumulation than basal clustering on low-productivity sites, regardless of stand stocking.

The strength of species richness as a predictor of live aboveground biomass, relative to the evolutionary diversity metrics, is consistent with another analysis of forest inventory plots across a broad scale (Paquette and Messier, 2011). Species richness is clearly a good indicator of the ability of forests to accumulate standing biomass on lower-productivity and lower-density stands, although it is not always the best predictor by site-productivity/relative density combinations or by geographic region. Like phylogenetic diversity, species richness is an indicator of functional richness, which appears to be the most important attribute of functional diversity for explaining standing biomass in low-density stands across site productivity classes. Apparently, having a community species composition that represents a greater amount of niche space is important for maximizing standing biomass as stands develop toward the self-thinning line (i.e., high relative density). Functional divergence, as quantified by phylogenetic species clustering, is a better predictor of variation in standing biomass on higher-density, lower-productivity sites, as noted above. Statistical models combining metrics representing each of the three functional diversity components, along with relative density as an indicator of successional status, predicted more than half the variation in live aboveground biomass on low-productivity sites nationally, and nearly half the variation on medium- and high-productivity sites. With one exception, models at the regional level also explained more than 50% of live aboveground biomass variation on low-quality sites, with some predicting more than 65%. Two of the ecoregions in which the models explained the least standing biomass variation are areas with relatively low tree overall species richness (Temperate Desert, SR = 68; Temperate Steppe, SR = 82), while ecoregions with better models tended to have higher overall species richness (e.g., Subtropical, SR = 186; Warm Continental, SR = 101). This underscores the importance of the diversity and composition of the regional species pool in determining plot-level relationships between biodiversity and productivity: Diverse species pools are more likely to include species with higher growth rates than smaller pools and are more likely to contain species better adapted to a greater array or environmental conditions (Fridley, 2001).

The findings reported here have particular relevance in the context of climate change (International Panel on Climate Change, 2007; National Climate Assessment and Development Advisory Committee, 2013), which appears to be forcing changes in the distributions of forest tree species (Woodall et al., 2009; Zhu et al., 2012) and may in turn be affecting regional patterns of plot-level forest biodiversity (Potter and Woodall, 2012). The importance of biodiversity for the functioning of ecosystems appears closely coupled to environmental unpredictability and complexity (Fridley, 2001), so biodiversity may play a significant role as a stabilizer of ecosystem processes in the face of largely uncertain global environmental change (Schlapfer et al., 1999; Schwartz et al., 2000). The "insurance hypothesis" (Tilman, 1999; Yachi and Loreau, 1999), for example, suggests that biodiversity provides a buffer against environmental fluctuations because species respond differently to these fluctuations, leading to more predictable aggregate ecosystem properties. Therefore, while at least some minimum number of species is essential for ecosystem functioning under constant conditions, a larger number is probably essential for maintaining the stability of ecosystem processes in changing environments (Loreau et al., 2001). Maximizing phylogenetic diversity, however, may be a better bet-hedging strategy during a future of climate change because doing so would be more likely to maximize community feature diversity (Forest et al., 2007) and increase ecosystem stability by ensuring that sufficient ecological strategies are represented in a community to ensure its persistence in the face of changing conditions (Cavender-Bares et al., 2009). The results of the current study suggest that phylogenetic biodiversity metrics, when considered along with site quality and stand stocking, provide a valuable tool for predicting the ability of forests to perform at least one important ecological function, biomass accumulation. These metrics serve as indicators of forest ecosystem function that vary by geographic region and by site quality, which can be applied to guide selection of appropriate management strategies to maximize the ability of forest ecosystems to maintain their functional attributes as environmental conditions change in ways that may be unexpected.

Given the novel application of evolutionary diversity metrics in the context of forest management in this study, future refinement and potential application are warranted. Future work, using the framework described here, should further elucidate the relationship between biodiversity and other forest ecosystem functions beyond live aboveground biomass (e.g., non-woody forest carbon pools) across broad-scales. This study focused on plot-level live aboveground biomass at a single point in time, but forest productivity can be measured as an increase in biomass over time. Newly emerging remeasured plot data from the FIA plot network could allow for the explicit assessment of whether and where biodiversity is associated with explicit metrics of live aboveground biomass accumulation and associated carbon stock changes. For example, additional analyses could consider belowground biomass, soil nutrient characteristics, and forest resistance to invasion by non-native plant species. The relationship between biodiversity metrics and forest functional diversity, based on tree species life-history characteristics, could also be examined (Paquette and Messier, 2011). In the context of forest management, it is the low-productivity forest sites in areas of the western U.S. that have been suffering from long-term droughts with widespread mortality (National Climate Assessment and Development Advisory Committee, 2013). Management decisions regarding tree species selection may have another metric to consider (e.g., phylogenetic species clustering) beyond species richness that may enhance live aboveground biomass accumulation on low quality sites that are facing potential climate-change induced events (e.g., droughts). Although forest managers may never directly work with measures of evolutionary diversity, measures of evolutionary diversity may be used in future development of management guidelines especially in forests where biomass accumulation or climate change adaption are priority objectives. Foresters make conscious decisions regarding the selection of tree species during most management activities which provide an avenue for adaptation to climate change (Pedlar et al., 2012). It is during this future selection process that evolutionary diversity metrics may come to bear when foresters are faced with the potential for novel climates/disturbances events. As metrics of evolutionary diversity are expected to be good surrogates for the diversity of tree functional attributes, incorporation of this fundamental information into appropriate forest management activities (e.g., biomass management on low quality sites) should increase as management complexities increase (e.g., climate change adaptation).

5. Conclusions

In certain situations and locations across the U.S., evolutionary diversity metrics supply additional information about forest stands beyond that of simple species richness counts. The additional information can potentially include critical insight into tree functional attributes related to evolutionary diversity. As forest managers are increasingly examining novel combinations of tree species, site qualities, and stand stocking to manage for emerging societal demands (e.g., biomass production, carbon sequestration, or climate adaptation), metrics of evolutionary diversity may increasingly play a role. Evolutionary diversity measures may be most critical for evaluating management direction on low quality and/or poorly stocked sites in areas not previously considered for forest management activities. It is these sites where biodiversity is most strongly associated with variation in live aboveground tree biomass, consistent with the expectation that the coexistence of functionally different species increases forest productivity in less productive and more stressful environments. Additional research using remeasured FIA plots should assess the regional relationships between biodiversity metrics and additional stand-level forest functional attributes, including growth and productivity (i.e., biomass change over time).

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Appendix A

The phylogenetic supertree used in these analyses, described in Potter and Woodall (2012), was based on the Angiosperm Phylogeny Group (APG) II classification of flowering plant families (Angiosperm Phylogeny Group, 2003), with the BLADJ (Branch Length ADJustment) module in Phylocom 3.41 (Webb et al., 2008) used to assign ages to nodes in this supertree based on fossil and molecular estimates (Wikström et al., 2001), with undated nodes spaced evenly between dated nodes to minimize variance in branch lengths. To improve the resolution of the phylogenetic supertree to the species level, and to incorporate gymnosperms, we surveyed molecular systematic and paleobotanical studies of the families and genera that encompass North American tree species, and of the higher-level gymnosperm groups (see Potter and Woodall, 2012). We added dated node constraints to the supertree topology where possible, and then re-ran the BLADJ algorithm in Phylocom to again set the ages of undated nodes evenly between dated nodes for the supertree.

Appendix B

The relative density (RD) of live trees on every plot is a function of stand density index (*SDI*) (Reineke, 1933; Long, 1985; Ducey and Larson, 2003) and maximum *SDI* (Woodall et al., 2005). *SDI* is defined in stands with non-Gaussian diameter distributions as:

$$SDI = \Sigma tph_i (DBH_i/25)^{1.6} \tag{B.1}$$

where DBH_i is the midpoint of the *i*th diameter class (cm) and tph_i is the number of trees per hectare in the *i*th diameter class (Shaw, 2000).

In order to determine a RD, the *SDI* of a stand is typically compared to an empirically observed, species-specific maximum *SDI* for determining the stand's RD. Woodall et al. (2005) proposed a methodology to estimate stand specific maximum *SDI* regardless of species mixture by using the mean specific gravity of all trees in the stand to estimate a stand's maximum *SDI*:

$$E(SDI_{Max}) = 3546.7 - 3927.3(SG_m) \tag{B.2}$$

where $E(.)$ is statistical expectation and SG_m is the mean specific gravity for all trees in each plot. The higher a species' specific gravity, the higher its modulus of elasticity within its bole, the more foliage that can be supported in its crown, and the less trees per unit area needed to support a site-limited amount of leaf area (Dean and Baldwin, 1996). Although there is emerging work (Ducey and Knapp, 2010) that may improve the coefficients of the Woodall et al. (2005) model at regional scales, the national coefficients proposed by Woodall et al. (2005) should prove adequate for a nationwide analysis. The RD of all study plots was determined as current *SDI* (Eq. (B.1)) divided by potential maximum *SDI* (Eq. (B.2)).

Appendix C. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2013.06.026.

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